

# SEXUAL DIMORPHISM, DISPERSAL PATTERNS, AND BREEDING BIOLOGY OF THE TAIWAN YUHINA: A JOINT-NESTING PASSERINE

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**ABSTRACT.**—We studied the breeding ecology of Taiwan Yuhinas (*Yuhina brunneiceps*) at the Highlands Experiment Farm at Meifeng, National Taiwan University, in 1995 and from 1997–2002. The Taiwan Yuhina is a joint-nesting, cooperatively breeding species endemic to Taiwan. Males had significantly longer wing chords and tail lengths than females, probably due to sexual selection. Males also had a longer residence time at Meifeng than their female mates, which could be explained by philopatry being greater in males. Alpha males had a significantly longer residence time at Meifeng than beta males, but this was not the case for females, because females did not remain in the same group as males did after their mates disappeared. The breeding season was approximately 6 months long and multiple brooding was common. Nest building took 3 days, egg laying occurred over 3–4 days, the average incubation period was 14 days, and the nestling period was 12 days. Breeding success did not decrease later in the breeding season. Maximum longevity was 12 years, and the estimate of average annual overwinter survival rate for adults at Meifeng was 74%. Received 3 August 2005, accepted 3 May 2006.

The Taiwan Yuhina (*Yuhina brunneiceps*), a Timaliine babbler, is a resident bird species endemic to subtropical Taiwan (Clements 2000). Male and female yuhinas are morphologically indistinguishable in the field. Joint-nesting behavior in yuhinas was first described by Yamashina (1938). Recently our group reported the social system (including joint nesting) and reproductive success (Yuan et al. 2004), incubation behavior (Yuan et al. 2004, 2005), and habitat selection (Lee et al. 2005) of yuhinas from a 7-year intensive study. Yuhinas formed breeding groups of 2–7 individuals; group-size mode was four. The yuhina is the only known passerine species to adopt a joint-nesting strategy for a large proportion of its nests (Vehrencamp and Quinn 2004).

The majority (69%) of passerine species have been considered sexually monomorphic (Barraclough and Harvey 1995); however, for many avian species there are subtle sexual differences in plumage color and morphology (Mays et al. 2006). Animals that live in

groups usually establish hierarchies, and members of different hierarchical levels often differ in terms of body size and age. Therefore, morphological and age comparisons between individuals of different sexes and hierarchical levels will shed light on the extent of sexual selection and the process of group formation. In this paper we describe the morphological differences between male and female yuhinas, residence times of different sexes and hierarchies, breeding chronology, longevity, and adult survival rate.

## METHODS

We studied a population of yuhinas at the Highlands Experiment Farm at Meifeng, National Taiwan University, in central Taiwan (24° 05' N, 121° 10' E; 2,150-m elevation) during 1995 and from 1997–2002. The study area is described in detail elsewhere (Yuan et al. 2004).

During this study, we color-banded 252 adult yuhinas. We measured bill, head (from the back of the cranium to the upper bill tip), tarsus, relaxed wing chord, flattened wing chord, and tail length; crest height (from the base of the bill to the tip of the longest crest feather) and width (above the eyes); and the weight of each captured adult. A 20- to 70- $\mu$ L blood sample was collected from the brachial vein of each adult and juvenile. Each sample was transferred into 500- $\mu$ L Queen's lysis buffer (Seutin et al. 1991) and frozen at

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–20°C until analyzed. Sex was tentatively assigned in the field based on observations of singing and copulation and later verified using sex-specific genetic markers (Fridolfsson and Ellegren 1999).

We defined a breeding group as a set of individuals exhibiting parental behavior toward the young of a single nest. Within each group, there was a linear hierarchy of socially monogamous pairs. Dominance hierarchies were easily determined by observing chasing and displacement behavior among group members (Yuan et al. 2004). We monitored the breeding chronology of 4, 6, 10, 11, and 13 groups in 1997, 1998, 1999, 2000, and 2001, respectively. Mayfield nest survival rates (Mayfield 1961, 1975) for different months were ascertained by intensively monitoring 13 breeding groups in 2001. Nest status was checked at 2- to 10-day intervals in different years. Predation events were determined by checking whether there were eggs, remains of eggs, or nestlings left in the nest. We assumed that there was no partial predation at yuhina nests, which was reasonable because the eggs and nestlings are rather small compared to those of their predators. We confirmed this assumption later by video-monitoring nests.

To estimate the adult overwinter survival rate, we monitored the fate of 125 banded individuals. For the years 1997–1998, 1998–1999, 1999–2000 and 2000–2001, we divided the number of banded birds that survived to the second year by the number of banded birds present in the first year. Following Vehrencamp et al. (1988), we identified six categories of disappearance: one of a mated pair; a dominant mated pair; an unmated bird; a non-breeding bird; a bird of uncertain status; and an entire group. We only counted the first two categories as mortalities; the others were more likely to have dispersed.

In 1990, 10 adult yuhinas were banded at Meifeng as part of a previous study (C.-W. Yen pers. comm.). Recaptures of these birds were used to estimate long-term survival. Because most birds were banded as adults, we could not determine their exact ages. Instead, we calculated minimum residence time at Meifeng. For banded birds present in 2000 and 2001, we determined the number of years in residence from the date of banding. Birds

present in both years were counted only once (in 2001).

Statistical analyses were performed using SAS software, ver. 8 (SAS Institute, Inc. 2000). The morphological characteristics and residence times of mated males versus females, and of alpha versus beta males and alpha versus beta females, were compared using unpaired or paired (as appropriate) *t*-tests to determine whether there were significant differences between groups. Means are represented as  $\pm$  SD.

## RESULTS

The behavior of 118 individuals was observed in the field and their sexes were determined by genetic markers. We correctly identified the sex of all paired individuals in the field, including 53 males and 47 females. However, the sex of unpaired individuals was difficult to determine solely by field observation. Of 18 unpaired birds, including 10 males and 8 females, the sex of only 6 males (and no females) was successfully determined by behavioral observation. Wing chord and tail length of males were significantly greater than those of females, but we detected no statistically significant differences in any other morphological variables (Table 1). Males also had a longer residence time than their mates ( $3.2 \pm 2.2$  versus  $2.4 \pm 1.7$  years; paired *t*-test:  $t_{16} = 2.36$ ,  $P = 0.033$ ). In addition, we found that, for a given group, alpha males had longer residence times than beta males ( $4.3 \pm 1.7$  versus  $2.8 \pm 1.3$  years; paired *t*-test,  $t_{12} = 2.92$ ,  $P = 0.014$ ). We found no difference in residence times of alpha versus beta females ( $3.2 \pm 1.9$  versus  $2.5 \pm 1.1$  years; paired *t*-test,  $t_{11} = 1.10$ ,  $P = 0.30$ ).

The breeding season lasted approximately 6 months, beginning in March or April and ending in August or September. Weather and predation were the two major causes of nest failure. In 2000 and 2001, strong winds and heavy rains during typhoons and afternoon thunderstorms destroyed 58% ( $n = 12$ ) and 21% ( $n = 42$ ) of the nests, respectively. Predators caused the failure of 21% (2000) and 55% (2001) of nests. Confirmed predators of yuhina eggs and nestlings were Eurasian Jay (*Garrulus glandarius*) and Taiwan Sibia (*Heterophasia auricularis*).

Nest success did not decrease as the season

TABLE 1. Morphological measurements (mm, except for weight) of male and female Taiwan Yuhinas from 17 groups studied in 1995 and from 1997–2001 in Meifeng, Taiwan (24° 05' N, 121° 10' E). Significant between-gender differences are boldfaced.

Measurement	Male	Female	<i>t</i>	<i>P</i>
	Mean ± SD ( <i>n</i> )	Mean ± SD ( <i>n</i> )		
Bill	11.9 ± 0.3 (25)	11.9 ± 0.6 (28)	0.19	0.85
Head	29.7 ± 0.6 (30)	29.6 ± 1.3 (27)	−0.29	0.78
Tarsus	17.9 ± 0.6 (25)	17.8 ± 0.6 (28)	0.81	0.42
Wing chord				
Relaxed	62.0 ± 1.6 (27)	59.9 ± 1.4 (31)	5.26	<b>&lt;0.001</b>
Flattened	63.5 ± 1.6 (26)	61.9 ± 1.6 (31)	3.86	<b>&lt;0.001</b>
Crest height	27.4 ± 1.5 (13)	26.3 ± 1.2 (13)	1.76	0.10
Crest width	10.7 ± 0.7 (13)	10.6 ± 1.2 (9)	0.22	0.83
Tail	46.3 ± 1.9 (27)	45.3 ± 1.3 (31)	3.20	<b>&lt;0.001</b>
Weight (g)	12.5 ± 0.8 (22)	12.3 ± 0.8 (26)	0.98	0.33

progressed in 2001 (linear regression,  $F_{1,4} = 0.001$ ,  $P = 0.89$ ; Fig. 1), and multiple-brooding was common among yuhinas at Meifeng. In 1997, 1998, and 2000, at least 3 of 26 groups successfully raised chicks to fledging in three consecutive broods, and at least 4 groups produced two successful broods each. In 2001, one group made nine nesting attempts after prior attempts were destroyed either by inclement weather or predators. In 2000 and 2001, we found one and two cases, respectively, in which group members were building a new nest while still feeding fledged

young from their previous brood. Nest building took approximately 3 days and egg laying occurred over 3–4 days. Incubation averaged  $14.3 \pm 1.9$  days ( $n = 21$ ) and the nestling period was  $11.6 \pm 2.0$  days ( $n = 19$ ). Re-nesting attempts were usually initiated within  $17.5 \pm 2.6$  days ( $n = 7$ ) of fledging from the first nest if the nest was successful and within  $5.8 \pm 3.5$  days ( $n = 49$ ) if the nest failed.

Of the 10 adult yuhinas banded in 1990, we recaptured four in 1998 (i.e., they were >9 yr old). Only one of the four was seen in 1999, and this individual was seen again in 2001 (>12 yr old). The estimated average annual adult overwinter survival was  $74 \pm 5\%$  ( $n = 4$  yr and 125 individual-yr).

DISCUSSION

At Meifeng, breeding males had longer residence times than did the females. Alpha males had longer residence times than beta males, but female dominance was not correlated with residence time. The longer residency of alpha males is likely because males need to queue into the groups to become dominants (Kokko and Johnstone 1999). The difference in male and female residence times could be explained by our observation that female status depended on the status of their mates: when paired alpha females disappeared, most of their mates retained their alpha status and found a new mate, but, when paired alpha males disappeared, few of their mates retained their dominant status (Yuan et al. 2004). Females had shorter residence times than their

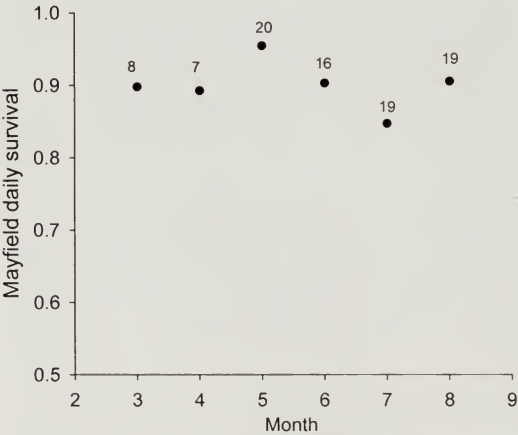


FIG. 1. Mayfield daily survival of Taiwan Yuhinas in different months of 2001 at Meifeng, Taiwan (24° 05' N, 121° 10' E). Survival did not decrease later in the breeding season. Sample size (nests) is shown above each point; month number corresponds to month sequence in a calendar year (i.e., 2 = February, 3 = March, etc.).



mates, possibly because females dispersed farther and searched for mates in larger areas, which might have increased their chances of encountering available dominant males. Alternatively, females might be forced to disperse when their mates die. Males remained in a group and queued for better breeding status for comparatively longer periods of time. Another explanation for the difference in male and female residence times might be different survival rates between males and females. Additional data on the relationship between age structure and group composition are needed, especially as they relate to sex and dominance.

The size difference between breeding male and female yuhinas could indicate that sexual selection has been occurring in this species. Larger body size is related to a better ability to compete for resources (Pusey and Packer 1997). Indeed, the body size of higher ranking male yuhinas was greater than that of lower-ranking males, but there was no such difference in females (Yuan et al. 2004). Because a female yuhina's status is dependent upon that of her mate, larger males might have an advantage because they can maintain higher breeding status and more easily attract mates.

Given that we did not find any evidence for a seasonal decline in nest success, and because harsh weather and predation were the main causes of nest failure, we reasoned that the combined effects of weather and predation pressure were consistent within a given breeding season. Therefore, the ability to reneest faster and more frequently is probably one of the main determinants of the yuhina's seasonal fecundity. As we have shown, yuhinas could make up to nine nesting attempts and were able to fledge multiple broods in a season. This result supports the recent argument that the number of nesting attempts made by songbirds is usually greater than formerly assumed (Farnsworth and Simons 2001, Grzybowski and Pease 2005). A seasonal trend in clutch size could have been another important factor affecting seasonal fecundity of yuhinas (e.g., Winkler and Allen 1996), although we did not have enough data to evaluate this possibility. Because yuhinas are too small to mob most of their predators and can reneest faster in larger groups, we suggest that the joint-nesting behavior is a bet-hedging strategy to cope

with the yuhina's highly variable environment, such as frequent typhoons and a high risk of predation; yuhinas invest less in single attempts and reneest faster to permit more nesting attempts (Yuan et al. 2004).

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